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Comparison of Leaf and Floral Morphology among Insular Endemics of *Pieris* (Ericaceae) on the Ryukyu Islands and Taiwan

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The floral and leaf morphology of Ryukyu *Pieris* were examined to determine the allopatric differentiation among the islands of Yakushima, Amamioshima, Okinawa, and Taiwan. The leaves of *P. koidzumiana* from Okinawa were narrower than those of other insular plants and were rheophytic, while *P. koidzumiana* from Amamioshima possessed the wider leaf characteristics of inland plants. *Pieris koidzumiana* populations from these two islands shared quite large and unconstricted corollas; however, they differed significantly in corolla size. *Pieris japonica* var. *yakushimensis* from Yakushima Island and *P. taiwanensis* from Taiwan had wider and smaller leaves than those of *P. koidzumiana*, as well as smaller and more constricted corollas. Morphological differentiation of *Pieris* plants on the Ryukyu Islands and Taiwan can be attributed to ecological differences among the islands, locations in a riverbank or inland habitat, and the presence of anthophilous insect communities on the islands.

Key words: corolla size, islands, leaf morphology, *Pieris*, the Ryukyu Islands

The genus *Pieris* of the family Ericaceae consists of shrubby plants and comprises seven species (Judd 1982, Mabberley 1997) or more (Yamazaki 1989, 1993) found in eastern Asia, eastern North America, and Cuba. In eastern Asia, its distribution ranges from the Himalayas to mainland Japan via the island arc of the Ryukyu Islands (the islands of Yakushima, Amamioshima, and Okinawa) and Taiwan (Fig. 1). A recent plastid DNA phylogeny indicated that the *Pieris* plants in these islands form a monophyletic group derived from a single ancestor (Setoguchi *et al.* submitted). Nevertheless, they are the subject of taxonomic controversy because of morphological variation in their leaves and flowers.

The *Pieris* species on Okinawa Island was initially recorded as *P. koidzumiana* Ohwi based on its larger flowers and linear leaves (Ohwi 1930). It was found in the riverbanks along the Fuku River on the island and is extinct in the wild at present. This species has also been treated as a subspecies or variety of *P. japonica* (Thunb.) D. Don ex G. Don (Masamune 1955, Hatsushima 1969) and included in *P. japonica* (Walker 1976, Judd 1982). On Amamioshima Island, *Pieris* plants were distributed on the summits of Mt. Yuwan and Mt. Jiwa, but the plants are possibly extinct in the wild at present. Hatusima (1969) recognized the Amamioshima Island plants as belonging to the same taxon as *P. koidzumiana* found on Okinawa Island and treated the plants on both islands as *P. japonica* (Thunb.) D. Don ex G.Don subsp. *koidzumiana* (Ohwi) Hatusima. On the other hand, *P. japonica* (Thunb.) D.

TABLE 1. Taxonomic treatments of *Pieris* plants distributed on the archipelago from Japan to Taiwan.

	Mainland of Japan	Yakushima Isl.	Amamioshima Isl.	Okinawa Isl.	Taiwan
Thunberg (1784)	*Andromeda japonica*	—	—	—	—
Don (1834)	*P. japonica*	—	—	—	—
Matsumura (1900)	—	—	—	—	*P. formosa*
Hayata (1911)	—	—	—	—	*P. taiwanensis*
Ohwi (1930)	*P. japonica*	—	—	*P. koidzumiana*	—
Masamune (1955)	*P. japonica*	—	—	*P. japonica* var. *koidzumiana*	—
Hatusima (1969)	*P. japonica*	*P. japonica*	*P. japonica* subsp. *koidzumiana*	*P. japonica* subsp. *koidzumiana*	*P. japonica* subsp. *taiwanensis*
Kitamura & Murata (1972)	—	—	—	—	*P. japonica* var. *taiwanensis*
Walker (1976)	*P. japonica*	—	—	*P. japonica*	—
Judd (1982)	*P. japonica*	—	—	*P. japonica*	*P. japonica*
Yamazaki (1989, 1993)	*P. japonica*	*P. japonica* var. *yakushimensis*	—	*P. koidzumiana*	—
Li *et al.* (1998)	—	—	—	—	*P. taiwanensis*

Don ex G. Don var. *yakushimensis* Yamazaki (Yamazaki 1993) and *P. taiwanensis* Hayata (Hayata 1912) were recognized on the islands of Yakushima and Taiwan, respectively (Table 1).

The *Pieris* plants from the Ryukyu Islands and Taiwan are defined by their vegetative and reproductive morphologies. *Pieris japonica* var. *yakushimensis* has oblong or oblong-lanceolate leaf blades, erect inflorescences with reflexed pedicels at anthesis, ascending pedicels at fructification, and elliptic-urceolate corollas ranging from 6 to 7 mm in length (Yamazaki 1993). *Pieris taiwanensis* is distinguished from the former taxon by its erect inflorescences with ascending pedicels at flowering and fruiting stages (Li *et al.* 1998). On the other hand, *P. koidzumiana* was described as having lanceolate leaves and large tubular-urceolate corollas of approximately 1 cm in length, based on observations of individuals from Okinawa Island (Hatusima 1969, Yamazaki 1993). However, these taxonomic characteristics on inflorescences and pedicels appear to be unstable for each *Pieris* plant on the islands of the Ryukyu Islands and Taiwan based on field observation (Setoguchi personal observation).

Niihara (2000) compared the floral morphology of *Pieris koidzumiana* from the islands of Okinawa and Amamioshima with that of *P. japonica* from Kagoshima Prefecture using approximately 20 flowers of typical morphology for each local population. The populations of the three localities were found to differ in corolla size. With respect to *P. koidzumiana*, moreover, Niihara (2000) suggested differences in floral morphology between Okinawa and Amamioshima islands: the plants of Amamioshima Island have longer and more obese (unstrictured) corollas than those of Okinawa Island.

Molecular phylogeny of the genus *Pieris* suggests that plants from the islands of Yakushima, Amamioshima, Okinawa, and Taiwan are monophyletic (Setoguchi *et al.* submitted). An accurate morphological comparison with a larger number of samples and statistical evaluation is needed among the *Pieris* populations that form the monophyletic group from the Ryukyu Islands and Taiwan.

Plastid DNA phylogeny has identified two distinct clusters within this monophyletic group, the

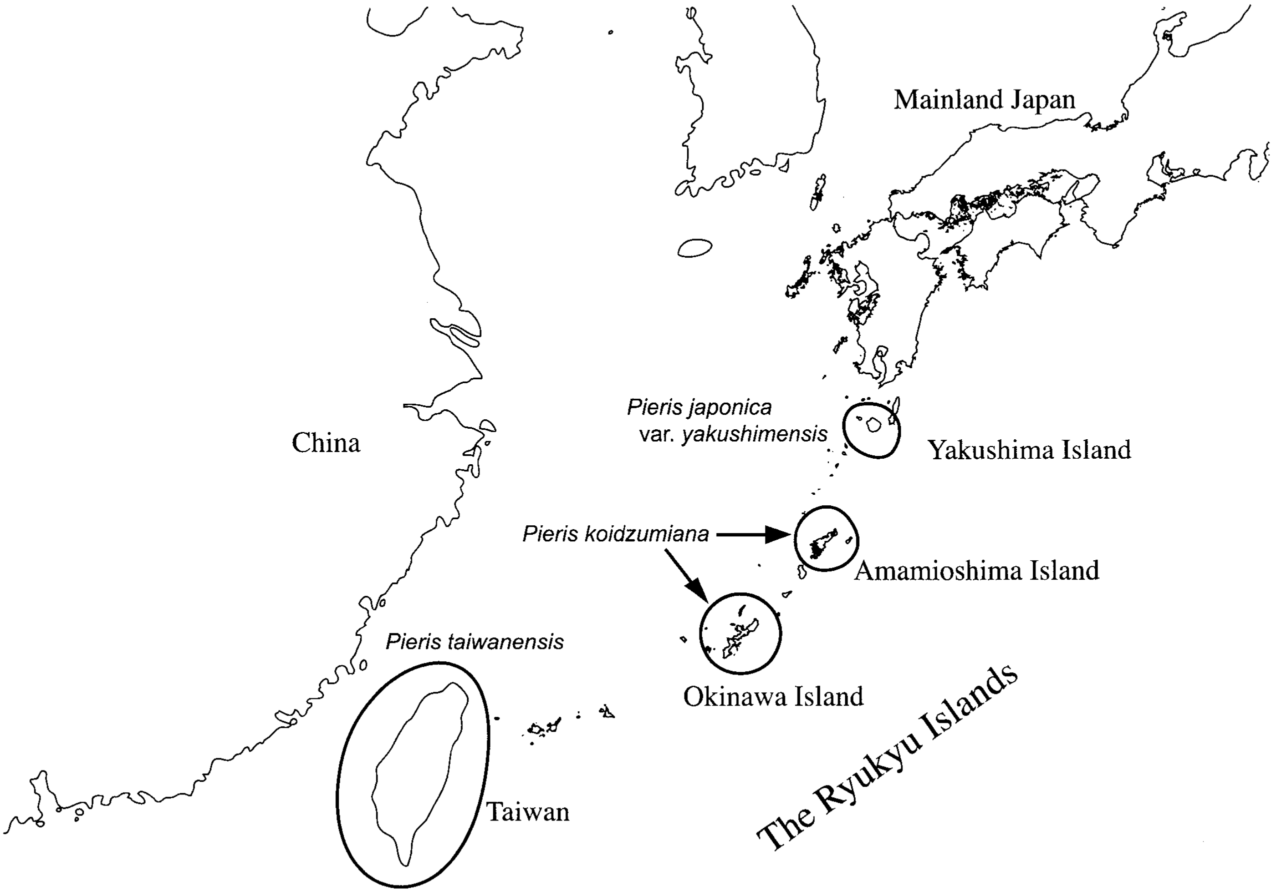

FIG. 1. Geographical distribution of the genus *Pieris* on the Ryukyu Islands and Taiwan, showing the distribution of *P. japonica* var. *yakushimensis*, *P. koidzumiana* and *P. taiwanensis*.

Yakushima - Amamioshima group and the Okinawa - Taiwan group, indicating that *Pieris koidzumiana* may be polyphyletic (Setoguchi *et al.* submitted). Moreover, *P. koidzumiana* from Amamioshima Island grew on mountain summits, while on Okinawa Island the plants grew along riverbanks, leading us to expect the plants from the former island to have much wider leaves than the rheophytic plants from the latter island.

In the present study, we compared the floral and leaf morphology of *Pieris* plants within the monophyletic group distributed on the islands of Yakushima, Amamioshima, Okinawa, and Taiwan. We report morphological differentiation among these islands, and discuss taxonomy as well as ecological factors that may affect morphology.

Materials and Methods

Pieris koidzumiana is considered to be extinct in the wild on the islands of Amamioshima and Okinawa; cultivation stocks are maintained only in botanical gardens, experimental forest stations, and private yards. We obtained *P. koidzumiana* samples from the cultivated stock at the Okinawa Forest Experiment Station, the Kagoshima Forest Experiment Station, the Kyoto Botanical Garden, the Makino Botanical Garden, and from private yards at Setouchi-cho on Amamioshima Island. Leaf and flower samples of *P. japonica* var. *yakushimensis* and *P. taiwanensis* were collected from plants in their natural habitats on Yakushima Island and Taiwan, respectively. We collected a shoot with fully matured leaves and flowers from each individual. The shoots were fixed

TABLE 2. Dimensions of leaf and floral morphologies in *Pieris* plants on the Ryukyu Islands.

Dimensions (Mean ± SD)	Yakushima	Amamioshima	Okinawa	Taiwan
Leaf				
Number of leaves examined	34	29	55	56
Blade length (a: mm)	46.0±4.2	69.4±9.0	63.8±8.2	53.9±7.2
Blade width (b: mm)	16.0±2.0	21.2±2.8	15.5±2.8	19.8±2.9
c/a	0.43±0.03	0.40±0.05	0.34±0.03	0.42±0.03
Leaf index (a/b)	2.90±0.33	3.29±0.33	4.14±0.61	2.74±0.30
Flower				
Number of flowers examined	104	87	118	79
Corolla length (L: mm)	7.2±0.9	10.8±0.9	9.6±1.1	8.0±0.3
Corolla width (Wmax: mm)	4.6±0.7	7.7±0.8	6.8±1.0	5.3±0.5
Wmin/Wmax	0.63±0.09	0.80±0.08	0.73±0.07	0.62±0.09

and kept in FAA for morphological measurements. Voucher specimens were deposited in the herbarium of Kyoto University (KYO).

For *Pieris koidzumiana*, 55 mature leaves and 118 flowers from 9 individuals from Okinawa Island, and 29 mature leaves and 87 flowers from 26 individuals from Amamioshima Island were supplied from cultivation stocks. Additionally, 34 mature leaves and 104 flowers from 34 individuals, and 56 mature leaves and 79 flowers from 12 individuals were used for *P. japonica* var. *yakushimensis* and *P. taiwanensis*, respectively.

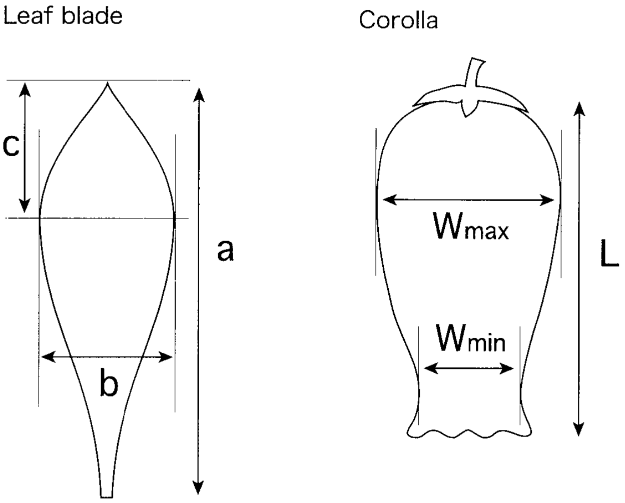

FIG. 2. Measurement of the leaf blade and corolla of *Pieris*: a, blade length; b, blade width; c, length between the widest point and the top of the blade; L, length of the corolla; Wmax, maximum width of the corolla; Wmin, minimum width of the corolla.

The fully matured leaves and flowers were measured using an electrical caliper square. Three morphological characteristics were measured for leaves and flowers (Fig. 2). The degree of leaf shape (c/a) was calculated as the ratio of the length between the widest point and the top of the blade (c) to blade length (a), representing the position of the maximum width of the leaf. Moreover, the leaf index (a/b) was also calculated as the ratio of blade length (a) to blade width (b) according to van Steenis (1981). The degree of corolla shape (Wmin/Wmax) was calculated as the ratio of minimum width (Wmin) to maximum width (Wmax), representing the relative degree of constriction at the orifice of the corolla.

The data were subjected to analysis of variance (one-way ANOVA) with Tukey's honestly significant difference test (Tukey's HSD) using the StatView J.5.0 software (SAS Institute Inc. 2000). In many cases, small numbers of leaf or flower materials were collected from each individual. Therefore, the analyses were subjected to the whole data sets of measurement of leaves or flowers from each individual. Principal Component Analysis (PCA) was also carried out for each data set of leaves and flowers using the Excel Principal Component Analysis

TABLE 3. Significant difference of morphological characters among populations. *: $p < 0.05$.

A. Length of leaf blade (a; above diagonal) and width of leaf blade (b; below diagonal).

	Yakushima	Amami	Okinawa	Taiwan
Yakushima	-	0.000*	0.000*	0.000*
Amami	0.000*	-	0.008*	0.000*
Okinawa	0.940	0.000*	-	0.000*
Taiwan	0.000*	0.133	0.000*	-

B. c/a (above diagonal) and leaf index (a/b; below diagonal).

	Yakushima	Amami	Okinawa	Taiwan
Yakushima	-	0.005*	0.000*	0.122
Amami	0.004*	-	0.000*	0.366
Okinawa	0.000*	0.000*	-	0.000*
Taiwan	0.371	0.000*	0.000*	-

C. Length of corolla (L; above diagonal) and width of corolla (Wmax; below diagonal).

	Yakushima	Amami	Okinawa	Taiwan
Yakushima	-	0.000*	0.000*	0.000*
Amami	0.000*	-	0.000*	0.000*
Okinawa	0.000*	0.000*	-	0.000*
Taiwan	0.000*	0.000*	0.000*	-

D. Wmin/Wmax (above diagonal).

	Yakushima	Amami	Okinawa	Taiwan
Yakushima	-	0.000*	0.000*	0.901
Amami		-	0.000*	0.000*
Okinawa			-	0.000*
Taiwan				-

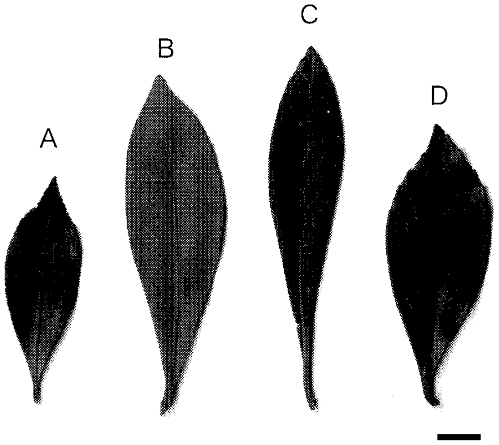

FIG. 3. Silhouettes of leaves of *Pieris* from the four islands of the Ryukyu Islands and Taiwan. A, Yakushima Island. B, Amamioshima Island. C, Okinawa Island. D, Taiwan. Scale bar = 1 cm.

ver. 4 software (Esumi Co., Tokyo, Japan).

Results

Leaf morphology

Variations in the size and dimensions of the leaves are indicated in Table 2 and the statistical evaluation is presented in Table 3. The silhouettes of *Pieris* leaves from each island are shown in Fig. 3.

The length and width of the leaf blades from Amamioshima plants were greater than those of plants from the other islands, and those of var. *yakushimensis* were the smallest. Significant differences were detected in all measurements between all plants, with the exception of leaf width between plants from Yakushima and Okinawa, and between plants from Amamioshima and Taiwan, the ratio of c/a between plants from Taiwan and Yakushima, and between those from Taiwan and Amamioshima, and leaf indices between plants from Yakushima and Taiwan ($p < 0.05$).

The leaf blades of *Pieris koidzumiana* from Okinawa were stenophyllous (Fig. 3), measuring approximately 63.8 mm in length and 15.5 mm in width, and the leaf index was determined to be 4.14 ± 0.61. The index of c/a was determined to be rheophyte leaves (van Steenis 1981) and also indicated that the maximum blade width was located more distally than in the other three collections (Fig. 4). In contrast, *P. koidzumiana* from Amamioshima had wider and longer leaf blades than plants from Okinawa, measuring approximately 69.4 mm in length and 21.2 mm in width with a leaf index of 3.29 ± 0.33. The leaves of var. *yakushimensis* and *P. taiwanensis* had a broader blade, and their leaf indices were 2.90 ± 0.33 and 2.74 ± 0.30, respectively. The leaf blades of var. *yakushimensis* were

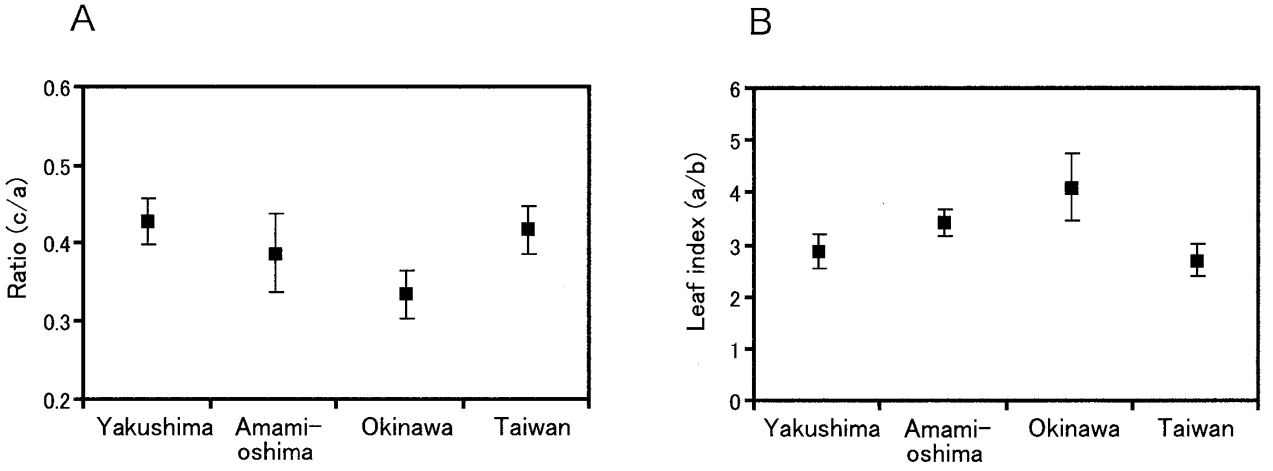

FIG. 4. Mean and standard deviation of the ratio (c/a) of length between the widest point and the top of the blade (c) to blade length (a), and the leaf index (a/b) of *Pieris* from the four islands of the Ryukyu Islands and Taiwan. A, c/a. B, a/b.

shorter than the others in length: approximately 46 mm long (Table 2).

PCA showed that leaves from the four islands were not clearly separated from each other, whereas the leaves from Okinawa Island were distinguished from those of Yakushima Island and Taiwan and slightly distinguished from those of Amamioshima Island (Fig. 5, Table 4). The first component was mainly based on leaf index (+0.6419 in factor loading), c/a (-0.5765), and length of leaf (+0.4364). Almost all leaves from Okinawa Island were distinct from those of Yakushima Island and Taiwan, whereas leaves from Amamioshima Island varied widely. The second component, based on leaf width (0.7656) and length (+0.6031), provided little information on differences among the insular *Pieris*.

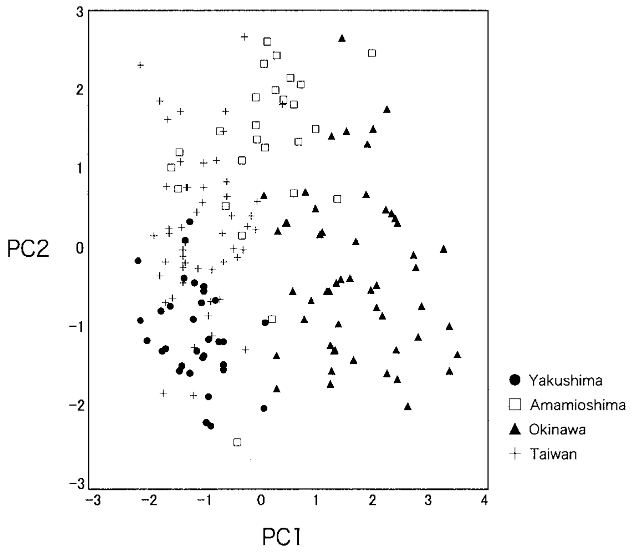

FIG. 5. Principal component analysis using four morphological characters of leaf.

Floral morphology

Variations in the size and dimensions of the corollas are indicated in Table 2 and the statistical evaluation is presented in Table 3. The gross morphologies of *Pieris* corollas from each island are shown in Fig. 6.

The corollas of *Pieris koidzumiana* from Okinawa and Amamioshima, measuring approximately 10 mm in length and 6.8 - 7.7 mm in width,

TABLE 4. Factor loading, eigenvalue, contribution, and accumulated contribution for principal components for leaf morphologies.

Characters	Component 1	Component 2
Factor loadings		
Length of leaf (a)	0.4364	0.6031
Width of leaf (b)	-0.2556	0.7656
c/a	-0.5765	-0.1038
Leaf index (a/b)	0.6419	-0.1984
Eigenvalue	2.08	1.46
Contribution (%)	51.90	36.46
Accumulated contribution (%)	51.90	88.36

were significantly larger than those of plants from Yakushima Island and Taiwan, which measured approximately 7.2 and 8.0 mm in length and 4.6 and 5.3 mm in width, respectively (Table 2, Figs. 6 and 7a, b). Moreover, the constriction at the corolla orifice of plants from Taiwan and Yakushima was significantly smaller (approximately 0.62 and 0.63 in Wmin/Wmax, respectively) than that of *P. koidzumiana* from Okinawa and Amamioshima (approximately 0.73 and 0.80, respectively; Table 2 and Fig. 7c). The flowers of *P. koidzumiana* from Amamioshima Island differed significantly from those of Okinawa Island in all dimensions examined (Tables 2 and 3).

PCA indicated that almost all corollas from Okinawa and Amamioshima Islands were separated from those from Yakushima Island and Taiwan, whereas corollas from Okinawa and Amamioshima Islands were weakly separated from each other (Fig. 8, Table 5). Corolla length (+0.6572 in factor loading), maximum corolla width (+0.6354), and Wmin/Wmax (+0.4054) contributed to the first component (Table 5). The second component, based on Wmin/Wmax (+0.9087), provided little information on the differences among the insular *Pieris*.

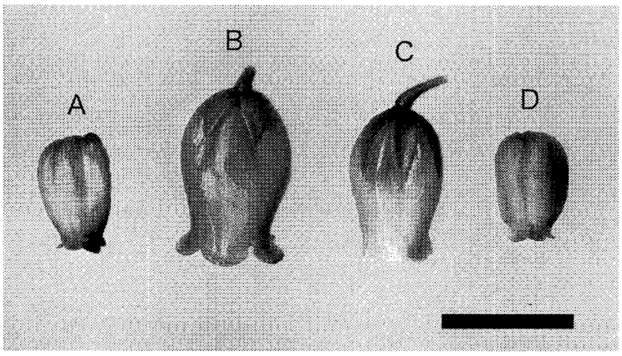

FIG. 6. Corollas of *Pieris* from the four islands of the Ryukyu Islands and Taiwan. A, Yakushima Island. B, Amamioshima Island. C, Okinawa Island. D, Taiwan. Scale bar = 1 cm.

Discussion

Pieris plants from the Ryukyu Islands and Taiwan differed distinctly in their leaf and flower shapes, particularly in the blade width, leaf indices, corolla size, and degree of constriction for the orifice of flowers.

The leaf index of *Pieris koidzumiana* from Okinawa Island was 4.14, suggesting to be rheophytic leaves according to van Steenis (1981). The position of the maximum leaf width (represented by c/a) was more distal than in the plants from the other three islands, also suggesting that this may be a characteristic of rheophytic plants, as described by van Steenis (1981). The high value of the leaf index and the low c/a ratio in this case may have resulted from adaptation to the riverbank and streambed environment of their original habitat on Okinawa Island through stenophyllous changes from an ancestral form. In contrast, the leaf index of *P. koidzumiana* from Amamioshima Island was 3.29, a value typical of inland plants. These two populations were significantly differentiated in leaf morphology as represented by the leaf index, although the leaf index values in both cases were higher than those of var. *yakushimensis* (2.90) and *P. taiwanensis* (2.74).

Moreover, morphological differentiation of *Pieris koidzumiana* between the islands of Amamioshima and Okinawa was recognized in corolla size and shape, with both the length and width of the corollas being greater in plants from Amamioshima Island than in those from Okinawa Island. The constriction at the orifice of the corolla was also weak in plants from Amamioshima Island.

Molecular phylogeny within the genus *Pieris* suggested that *P. koidzumiana* was paraphyletic; *P. koidzumiana* of Okinawa Island was monophyletic with *P. taiwanensis* in Taiwan, and *P. koidzumiana* of Amamioshima Island was clustered with *P. japonica* var. *yakushimensis* of Yakushima Island (Setoguchi *et al.* submitted). The morphological differentiation of *P. koidzumiana* between the islands of Amamioshima and Okinawa was consistent with the heterogeneity of the species. The morphological

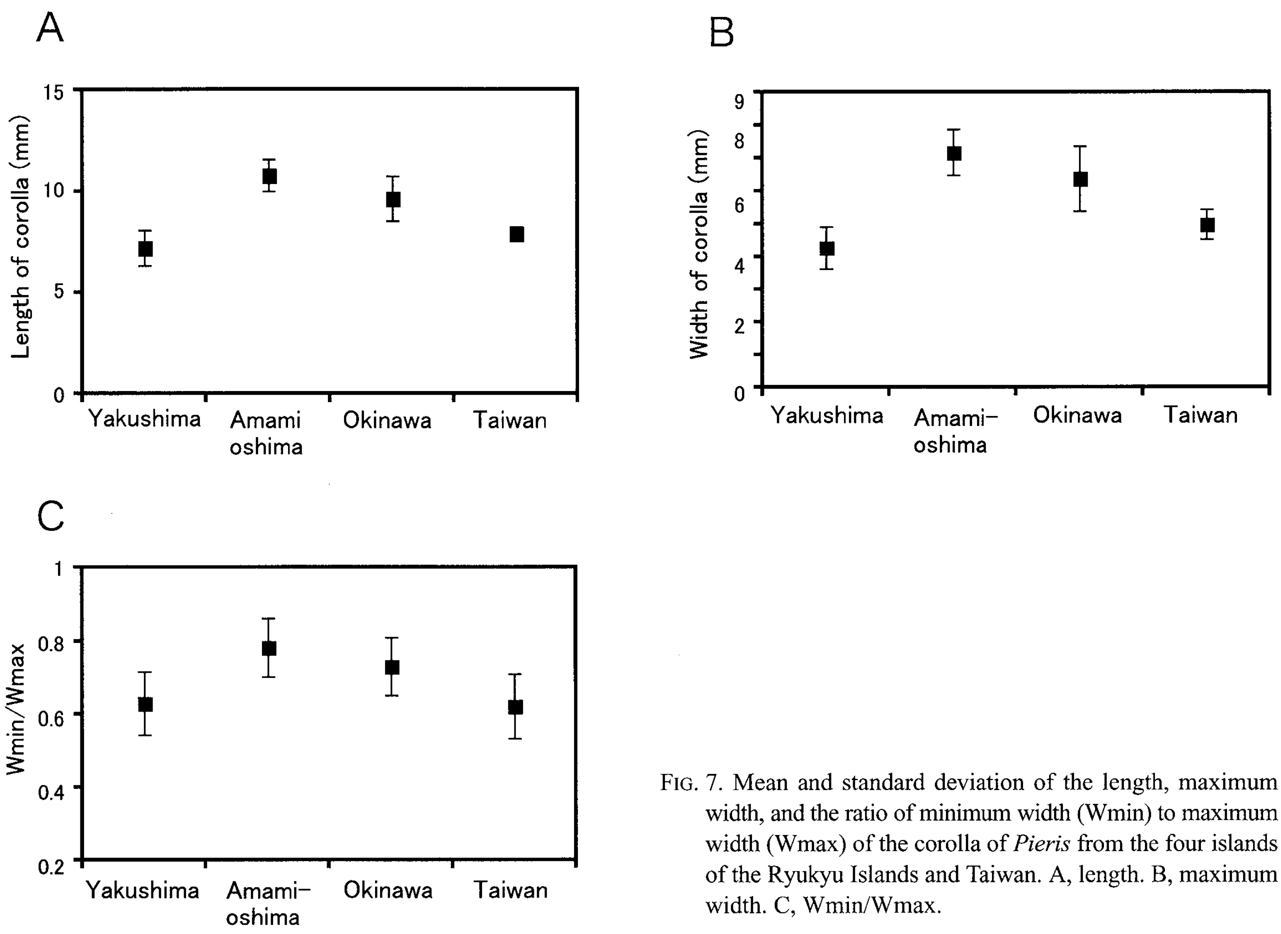

FIG. 7. Mean and standard deviation of the length, maximum width, and the ratio of minimum width (Wmin) to maximum width (Wmax) of the corolla of *Pieris* from the four islands of the Ryukyu Islands and Taiwan. A, length. B, maximum width. C, Wmin/Wmax.

characteristics of *P. koidzumiana*, such as larger corolla size (Hatusima 1969), should be regarded as convergence.

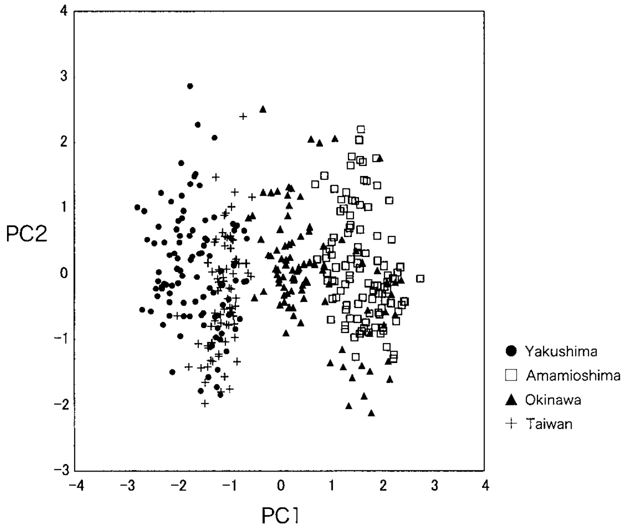

FIG. 8. Principal component analysis using three morphological characters of corolla.

Based on the above morphological and phylogenetic evidence, we conclude that the *Pieris* plants on Amamioshima Island should be treated as an independent taxon separate from the *P. koidzumiana* in Okinawa Island. Based on the taxonomy by Yamazaki (1989, 1993) and Li *et al.* (1998), which

TABLE 5. Factor loading, eigenvalue, contribution, and accumulated contribution for principal components for floral morphologies.

Characters	Component 1	Component 2
Factor loadings		
Length of corolla	0.6572	-0.2143
Maximum width of corolla	0.6354	-0.3582
Wmin/Wmax	0.4054	0.9087
Eigenvalue	2.14	0.78
Contribution (%)	71.40	26.12
Accumulated contribution (%)	71.40	97.53

recognized endemic species of *Pieris* on Okinawa Island and Taiwan, respectively, we should treat the plants of Amamioshima Island as a new species. However, Judd (1982) adapted *P. japonica sensu lato* for the monophyletic *Pieris* species of the Ryukyu Islands, Taiwan, and mainland Japan. In this sense, the insular *Pieris* in Amamioshima should be treated as an infraspecific taxon of *P. japonica*.

It is noteworthy that the measured morphological characteristics significantly differed within the monophyletic groups, *e.g.*, *Pieris koidzumiana* from Okinawa Island possessed a much larger corolla and narrower leaves than plants from Taiwan. The morphological differentiation may have arisen after allopatric diversification from a single ancestor. The geographic isolation of the islands, the environmental diversity of their habitats (rheophytic zone and inland, lower elevations and rocky mountain summits), and the anthophilous insect communities on the islands may have influenced the plant morphology. For example, the environmental pressure of a rheophytic zone could be responsible for the narrower leaves found on plants from Okinawa Island, and the nutrient-poor andesitic bedrock presumably led to smaller leaves on Yakushima Island. The convergence of the large corolla size of *P. koidzumiana* on Okinawa and Amamioshima Islands should be evaluated and may be ascribed to some adaptation of their pollinators. For example, the anthophilous insect communities on Okinawa and Amamioshima Islands are characterized by the absence of bumblebees (Sakagami & Ishikawa 1969, Kato 2000). Indeed, Inoue and Amano (1986) reported that changes of pollinators (*i.e.*, absence of bumble bees and pollinator shift from bumble bee into small bees [*e.g.*, *Lasioglossum*]) affected collora size in island system. A relationship between pollinator size and corolla size has also been suggested in mainland Japan (Suzuki 1992, Dohzono & Suzuki 2002, Dohzono *et al.* 2004) and other areas (Inouye 1978, 1980). The rich environmental diversity and the insularity found in the island system of the Ryukyu Islands and Taiwan can be assumed to have played an important role in the morphological differentiation of *Pieris* populations among the islands.

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